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TEMPORAL AND VERTICAL DISTRIBUTION OF BARK BEETLES (COLEOPTERA: SCOLYTIDAE) CAPTURED IN BARRIER TRAPS AT BAITED AND UNBAITED LODGEPOLE PINES THE YEAR FOLLOWING ATTACK BY THE MOUNTAIN PINE BEETLE

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Abstract

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Bark beetles were trapped for two summers in a mature stand of lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae), infested by mountain pine beetle, *Dendroctonus ponderosae* Hopkins, near Princeton, British Columbia. Columns of flight-barrier traps were suspended next to uninfested live trees and from dead brood trees containing new adult beetles. The brood trees had been treated in the previous year with mountain pine beetle pheromone bait alone or in combination with *Ips pini* Say (Coleoptera: Scolytidae) pheromone bait and subsequently killed by mountain pine beetles. A total of 3376 individuals from 30 species of Scolytidae were captured in the traps. Most of the species for which lodgepole pine is a nonhost or occasional host were captured in low numbers (one or two specimens). The most abundant species (>30 individuals) were *D. ponderosae*, *I. pini*, *Hylurgops porosus* LeConte, *Pityogenes knechteli* Swaine, and *Trypodendron lineatum* Olivier. The treatments affected captures of mountain pine beetles and *I. pini* but only in the year when trees were either unbaited or baited simultaneously for mountain pine beetle and *I. pini*. There were significant differences among the five most abundant species in the mean heights and mean Julian dates of capture. In addition to host condition requirements, these differences reflected partitioning of the food and habitat resource and competitive interactions among species. There was no interaction between treatment and trap height, indicating that treatment did not affect the height distribution of flying beetles.

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Résumé

Les scolytes ont été capturés au cours de deux saisons estivales dans une forêt de pins tordus latifoliés (*Pinus contorta* var. *latifolia*) et d'épinettes d'Engelmann (Pinaceae) matures infestés par le Dendroctone du pin argenté (*Dendroctonus ponderosae* Hopkins). La forêt est située près de Princeton, en Colombie-Britannique. Des colonnes de pièges (pour le piégeage en vol) ont été suspendues à côté d'arbres sains (non infestés) et à des arbres foyers morts abritant une nouvelle génération d'insectes adultes. Les arbres foyers avaient été traités l'année précédente avec un appât à base de phéromones du Dendroctone du pin argenté, seul ou combiné à un appât à base de phéromones du *Ips pini* Say (Coleoptera : Scolytidae), à la suite de quoi ces arbres avaient été tués par les dendroctones. Un total de 3376 spécimens appartenant à 30 espèces différentes de scolytes ont été capturés dans les pièges. La plupart des espèces qui ne parasitent pas le Pin tordu latifolié ou ne le font qu'occasionnellement ont été capturées en faible nombre (un ou deux spécimens). Les espèces les plus abondantes (plus de 30 représentants) étaient *D. ponderosae*, *I. pini*, *Hylurgops porosus* LeConte, *Pityogenes knechteli* Swaine et *Trypodendron*

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lineatum Olivier. Les traitements n'ont affecté les captures de dendroctones du pin argenté et de *I. pini* que lorsque les arbres n'avaient pas été appâtés ou avaient été appâtés simultanément pour le Dendroctone du pin argenté et *I. pini*. On a constaté des différences importantes entre les espèces les plus abondantes pour ce qui est des hauteurs moyennes et des dates juliennes moyennes de capture. Ces différences reflétaient la diversité des exigences concernant la condition de l'hôte mais aussi la séparation des ressources alimentaires et de l'habitat ainsi qu'une compétition entre les différentes espèces. On n'a observé aucun lien entre le traitement et la hauteur du piège, ce qui montre que le traitement n'a pas affecté la distribution verticale des insectes en vol.

Introduction

Over 50 species of scolytid bark beetles breed in lodgepole pine, *Pinus contorta* var. *latifolia* Engelmann (Pinaceae), in Canada (Bright 1976). Depending on host requirements and geographic distribution, only a subset of these scolytid species is expected to be present in any given stand of lodgepole pine infested by the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae) (Bright 1976) (authorities for all insect taxa are given in Table 1).

Lodgepole pines are invaded by various secondary bark beetles subsequent to being attacked by mountain pine beetle (Wood 1982; Safranyik *et al.* 1996). The secondary attackers breed in areas of phloem unoccupied by mountain pine beetle. Some may reattack the same or other dead trees in the year following tree mortality. Hence, both emerging and attacking adults of some scolytid species may be found in a tree during the year following mountain pine beetle attack. Although partitioning of the phloem resource among species occurs (Savoie 1996; Safranyik *et al.* 1999), attacks by some species often intermingle with those of the mountain pine beetle, resulting in competitive interactions.

The temporal and vertical distributions of flying bark beetles may be used as indices of attack distribution and potential overlap of attacks in studies of resource partitioning and competitive interactions. These distributions may be affected by the complex pattern of colonization of trees under attack and further complicated by the application of pheromones (Safranyik *et al.* 1999).

The objectives of this study were to determine the temporal and height distributions of dispersing bark beetles at pheromone-baited and unbaited lodgepole pines the year following mountain pine beetle attack, with emphasis on commonly occurring species.

Methods

The field sites were located near Saturday Creek, approximately 50 km southwest of Princeton, British Columbia (49°28′N, 120°31′E). The overstory was primarily 60- to 100-year-old lodgepole pine with scattered Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae). Two locations were used. In 1995, traps were placed in a patch of lodgepole pine, 23–36 cm DBH (diameter at a height of 1.3 m), 25–30 m high, and located on an east-facing slope. During 1996, the traps were placed about 1 km to the southeast of the 1995 site on a southeast-facing slope in a pure lodgepole pine stand, 15–30 cm DBH and 18–20 m high.

Four sets of flight-barrier traps were deployed on 11 May 1995. Each trap consisted of two 30 × 30 cm, clear, 3-mm Plexiglas windows joined in a cross, fixed diagonally above a square metal funnel leading to a collecting jar. Each of the four sets consisted of six traps, which were hung from the rungs of a rope ladder suspended from

TABLE 1. Mean heights, mean capture dates, and numbers (*n*) of Scolytidae (Coleoptera) species captured in flight-barrier traps.

	Height (m)				Capture date			
	1995		1996		1995		1996	
	n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Abundant species								
Dendroctonus ponderosae Hopkins	500	8.5 (0.2) *b*	327	3.6 (0.1) *bc*	500	227.8 (11.2) *a*	327	227.4 (12.0) *a*
Hylurgops porosus LeConte	54	5.6 (0.5) *c*	106	3.0 (0.2) *c*	54	163.7 (21.4) *e*	106	166.0 (21.9) *d*
Ips pini (Say)	183	10.4 (0.3) *a*	839	4.0 (0.1) *b*	183	206.7 (21.1) *c*	839	198.7 (37.9) *b*
Pityogenes knechteli (Swaine)	379	11.3 (0.2) *a*	714	5.6 (0.1) *a*	379	211.4 (11.7) *b*	714	179.7 (25.5) *c*
Trypodendron lineatum (Olivier)	82	4.5 (0.5) *d*	48	3.1 (0.3) *c*	82	170.6 (32.0) *d*	48	160.0 (24.8) *d*
Rare species								
Dendroctonus brevicomis Leconte	0		1	1.0	0		1	202.0
Dendroctonus pseudotsugae Hopkins	1	6.0	0		1	163.0	0	
Dendroctonus murrayanae Hopkins	5	3.0 (0.9)	0		5	162.2 (10.1)	0	
Dendroctonus valens LeConte	0		7	1.6 (0.2)	0		7	176.0 (9.0)
Dryocoetes autographus (Ratzeburg)	4	11.25 (2.2)	13	2.2 (0.3)	4	216.3 (32.6)	13	202.8 (16.5)
Dryocoetes confusus Swaine	0		1	1.0	0		1	190.0
Gnathotrichus sulcatus LeConte	0		1	3.0	0		1	179.0
Hylastes gracilis LeConte	13	5.8 (0.7)	4	4.3 (2.1)	13	169.5 (6.9)	4	184.8 (9.9)
Hylastes macer LeConte	1	9.0	5	4.2 (1.3)	1	163.0	5	190.4 (10.2)
Hylastes nigrinus (Mannerheim)	1	3.0	9	2.8 (0.9)	1	211.0	9	196.6 (19.0)
Hylastes ruber Swaine	2	2.25 (1.1)	0		2	177.0 (0.0)	0	
Hylastes reticulatus Wood	4	6.0 (1.4)	0		4	166.5 (6.0)	0	
Hylastes subcostulatus Mannerheim	5	6.0 (2.1)	0		5	163.0 (0.0)	0	
Ips emarginatus (LeConte)	2	6.0 (4.2)	2	3.0 (2.8)	2	178.0 (33.0)	2	265.0 (17.0)

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TABLE 1 (*concluded*).

	Height (m)				Capture date			
	1995		1996		1995		1996	
	n	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Ips latidens (LeConte)	9	6.0 (0.5)	1	9.0	9	189.1 (10.3)	1	179.0
Ips mexicanus (Hopkins)	9	4.7 (0.8)	1	1.0	9	192.9 (21.9)	1	150.0
Ips perturbatus (Eichoff)	1	15.0	0		1	211.0	0	
Orthotomicus caelatus (Eichoff)	2	3 (0.0)	1	3.0	2	187.0 (24.0)	1	190.0
Polygraphus rufipennis (Kirby)	1	9.0	0		1	192.0	0	
Pityopthorus (Eichoff) spp.	1	3.0	25	4.6 (0.6)	1	226.0	25	194.2 (22.9)
Pityokteines ornatus (Swaine)	0		1	5.0	0		1	179.0
Scierus annectans LeConte	0		2	3.0 (2.8)	0		2	163.0 (0.0)
Scolytus tsugae (Swaine)	2	9.0	0		2	178.0 (33.0)	0	
Scolytus ventralis LeConte	0		3	6.3 (0.8)	0		3	229.0 (5.6)

NOTE: Columns of six traps were suspended from each of four *Pinus contorta* var. *latifolia* at Saturday Creek, British Columbia, in 1995 and 1996. Capture dates are given as julian dates. Mean heights and dates within a column and followed by the same letter are not significantly different (Newman–Keuls test, $P > 0.05$). The corresponding species are those of which at least 30 individuals were captured and were designated as the abundant species.

a pulley at the end of a 1-m-long yardarm. The yardarms were attached to the north sides of mature lodgepole pines (Safranyik *et al.* 1992) at a height of 16 m. The lowest traps were positioned at 1.5 m and the remainder at 3-m intervals from 3 to 15 m on the ladder. The support ropes were run through pulleys to facilitate lowering for inspection. Four unattacked lodgepole pines, separated by at least 15 m, were selected for baiting prior to mountain pine beetle emergence in 1994. Two of these trees, selected at random, were baited simultaneously with standard mountain pine beetle bait [*trans*- and *cis*-verbenol and (±)-*exo*-brevicomin] and *Ips pini* bait [(±)-ipsdienol and lanierone] (Phero-Tech Ltd., Delta, British Columbia). The other two trees were baited with standard mountain pine beetle bait. A set of traps was attached to each of the four baited trees. All baited trees were killed in 1994 by mountain pine beetle, and thus contained mountain pine beetle brood adults in 1995.

Four sets of six flight-barrier traps were put in place at the second site on 13–14 May 1996. Traps were hung at heights of 1, 2, 3, 5, 7, and 9 m because the trees were shorter than those used in 1995. Ladders were hung as in 1995 on two brood trees which had been baited simultaneously in 1995 for mountain pine beetle and *I. pini*, and thus contained mature adults in 1996, and on two unbaited live trees of similar size 15 m away from the baited trees.

Collections were made biweekly between 11 May and 27 September in 1995 and between 14 May and 8 October in 1996. All collections were preserved in 70% alcohol by trap and date until species identifications could be performed in the laboratory.

The trap data were divided into two groups for analysis: abundant (30 or more captured individuals) and rare species (fewer then 30 captured individuals). Each species in the abundant group was analyzed separately by year using analysis of variance (ANOVA) with model factors for bait treatment, trap height, and collection date, with a split-plot arrangement for the last two factors. Variations in the heights and dates of capture among species were analyzed with one-way ANOVA. Differences among means within years were compared using the Newman–Keuls test at $P \leq 0.05$. For analysis of collection dates, data were converted to day of year. Differences in mean heights and mean dates between years for each species were compared using a t test at $P \leq 0.05$. Prior to analysis, counts and dates of capture were transformed to $(X + 1)^{0.5}$. No analysis was done for the rare species, and only the means and standard deviations of the numbers captured by trap height or collection date are reported.

Results

Species Abundance. Thirty species of scolytids were trapped during the 2 years: 23 species in 1995 and 22 species in 1996 (Table 1). For all treatments, the most abundant species collected were *D. ponderosae*, *Hylurgops porosus*, *I. pini*, *Pityogenes knechteli*, and *Trypodendron lineatum*. The rare species were mainly represented by fewer than 10 individuals (Table 1). Lodgepole pine is not a known host for several of the rare species, such as *Dryocoetes confusus*, *Scolytus tsugae*, and *Scotylus ventralis*, and is only an occasional host of *Scierus annectans*, *Dendroctonus pseudotsugae*, and *Ips perturbatus* (Bright 1976). The majority of the other rare species prefer injured or freshly killed trees (*Dendroctonus murrayanae*, *Dendroctonus valens*, species of the genera *Hylastes* Erichson and *Hylurgops* LeConte, and *Gnathotrichus sulcatus*), branches, or thin bark (*Ips latidens* and species of the genera *Pityophthorus* Eichoff and *Pityokteines* Fuchs) (Bright 1976; Hopping 1961).

TABLE 2. Analysis of variance by treatment, trap height, and collection date for each of the five most abundant bark beetle species (Coleoptera: Scolytidae) captured in columns of six flight-barrier traps suspended from each of four *Pinus contorta* var. *latifolia* at Saturday Creek, British Columbia, in 1995 and 1996.

		1995			1996		
	Source	df	*F*	*P*	df	*F*	*P*
Dendroctonus ponderosae	Treatment (*T*)	1	0.46	0.51	1	5.14	0.04
	Trap height (*H*)	5	14.83	0.00	5	10.9	0.41
	$T \times H$	5	0.63	0.68	5	1.19	0.32
	Capture date (*D*)	7	78.09	0.00	9	16.77	0.00
	$T \times D$	7	1.51	0.17	9	3.71	0.00
	$H \times D$	35	5.61	0.00	45	1.13	0.32
Ips pini	Treatment (*T*)	1	0.59	0.46	1	5.1	0.04
	Trap height (*H*)	5	16.61	0.00	5	1.28	0.33
	$T \times H$	5	0.6	0.70	5	1.57	0.18
	Capture date (*D*)	7	101.92	0.00	9	22.94	0.00
	$T \times D$	7	1.62	0.14	9	3.85	0.00
	$H \times D$	35	6.38	0.00	45	1.32	0.15
Pityogenes knechteli	Treatment (*T*)	1	0.3	0.60	1	0.05	0.82
	Trap height (*H*)	5	1.03	0.44	5	1.03	0.44
	$T \times H$	5	0.34	0.89	5	0.3	0.91
	Capture date (*D*)	7	6.33	0.00	9	7.39	0.00
	$T \times D$	7	1.14	0.34	9	0.94	0.50
	$H \times D$	35	0.86	0.68	45	0.73	0.86
Hylurgops porosus	Treatment (*T*)	1	0.11	0.75	1	2.22	0.16
	Trap height (*H*)	5	2.57	0.08	5	3.08	0.05
	$T \times H$	5	0.58	0.71	5	2.51	0.04
	Capture date (*D*)	7	7.42	0.00	9	15.86	0.00
	$T \times D$	7	0.27	0.96	9	0.63	0.76
	$H \times D$	35	1.93	0.01	45	1.93	0.01
Trypodendron lineatum	Treatment (*T*)	1	0	1.00	1	1.47	0.25
	Trap height (*H*)	5	2.35	0.10	5	0.38	0.86
	$T \times H$	5	1.33	0.26	5	0.93	0.47
	Capture date (*D*)	7	5.43	0.00	9	3.47	0.00
	$T \times D$	7	0.62	0.74	9	1.2	0.31
	$H \times D$	35	1.79	0.02	45	1.04	0.44

Analysis of Abundant Species. The 1996 bait treatment resulted in significantly higher captures of mountain pine beetles and *I. pini* (276 and 564) than the unbaited controls (51 and 275) (Table 2).

Effects of trap height were significant for mountain pine beetle and *I. pini* in 1995 only and for *H. porosus* in both years (Table 2). Numbers of mountain pine beetles and *I. pini* peaked at 9 and 12 m in 1995, but both peaked at 3 m in 1996 (Table 3). Numbers of *H. porosus* and *T. lineatum* peaked within 3 m in both years, whereas captures of *P. knechteli* generally increased to peak at 9 m (Table 3).

Interactions of bait treatment with height were not significant for any of the abundant species, indicating that the relative abundance of these species in flight was not affected (Table 2).

There was variation among species in the capture height in both years (1995: $F_{4,1193} = 94.34$, $P \leq 0.0001$; 1996: $F_{4,2033} = 58.08$, $P \leq 0.0001$). The mean capture

TABLE 3. Mean numbers of the five most abundant bark beetle species (Coleoptera: Scolytidae) captured per tree in columns of six flight-barrier traps suspended from each of four *Pinus contorta* var. *latifolia* at six heights at Saturday Creek, British Columbia, in 1995 and 1996.

Trap height (m)	*Dpon*	*Ipin*	*Pkne*	*Hpor*	*Tlin*
		1995			
1.5	3.50*c*	0.00*c*	0.00*a*	1.25*ab*	7.25*a*
3	15.50*b*	2.25*b*	1.00*a*	5.75*a*	7.50*a*
6	32.00*a*	6.75*a*	9.50*a*	2.75*ab*	2.00*a*
9	40.00*a*	11.75*a*	28.75*a*	1.75*ab*	1.50*a*
12	19.00*b*	14.75*b*	27.75*a*	2.00*ab*	0.25*a*
15	16.00*b*	9.50*b*	27.75*a*	0.00*b*	2.00*a*
		1996			
1	9.00*a*	26.00*a*	14.25*a*	7.25*a*	0.75*a*
2	20.25*a*	49.50*a*	34.00*a*	6.50*a*	6.50*a*
3	22.75*a*	54.00*a*	18.00*a*	7.25*a*	2.75*a*
5	22.00*a*	29.75*a*	20.00*a*	2.00*a*	0.50*a*
7	8.50*a*	26.00*a*	36.50*a*	1.75*a*	0.50*a*
9	1.75*a*	24.50*a*	55.75*a*	1.75*a*	1.00*a*

NOTE: Means are based on combined data from the two bait treatments and two trees per treatment. For each year, means within a column followed by the same letter are not significantly different (Newman–Keuls test, $P > 0.05$). *Dpon*, *Dendroctonus ponderosae*; *Hpor*, *Hylurgops porosus*; *Ipin*, *Ips pini*; *Pkne*, *Pityogenes knechteli*; *Tlin*, *Trypodendron lineatum*.

heights were greater in 1995. As well, the mean capture heights for *H. porosus* and *T. lineatum* were significantly lower, and those for *I. pini* and *P. knechteli* significantly higher, than those for the mountain pine beetle in 1995. In 1996, the mean capture heights of mountain pine beetle, *I. pini*, *H. porosus*, or *T. lineatum* were not significantly different (Table 1). When maximum trap height was restricted to the highest common height in the two years (9 m), mean capture heights among years were still different for the abundant species (range in t values: $t_{923} = 2.61$, $P \leq 0.0001$ for *I. pini*, and $t_{869} = 40.80$, $P \leq 0.0001$ for *P. knechteli*).

There was variation in the dates (day of year) of capture among the abundant species (1995: $F_{4,1193} = 386.33$, $P \leq 0.0001$; 1996: $F_{4,2029} = 188.32$, $P \leq 0.0001$). In both years, the mean date of capture was earliest for *H. porosus* and *T. lineatum*, followed by *I. pini* and *Pityogenes knechteli*, with mountain pine beetle latest (Table 1). Peak flight (Table 4; Figs. 1*a*, 1*b*) and cumulative flight (Figs. 2*a*, 2*b*) occurred in the same order. There were differences in mean dates of capture between years for *I. pini*, *P. knechteli*, and *T. lineatum*, but not for the mountain pine beetle or *H. porosus* (range in t values: $t_{825} = 0.48$, $P > 0.05$ for mountain pine beetle, and $t_{1091} = 30.34$, $P \leq 0.0001$ for *P. knechteli*).

There was a significant interaction between treatment and date of capture of mountain pine beetle and *I. pini* in 1996 (Table 2). Early in the trapping period, baited trees generally captured the greatest numbers of both species.

Discussion

Two of the five common species of scolytids captured, *I. pini* and *P. knechteli*, are known cohabitants with mountain pine beetle in lodgepole pine (Hopping 1961; Poland 1993; Safranyik and Linton 1998; Safranyik *et al.* 1974, 1999). They mainly infest the

TABLE 4. Mean numbers of the five most abundant bark beetle species (Coleoptera: Scolytidae) captured per trap by date of capture in columns of six flight-barrier traps suspended from each of four *Pinus contorta* var. *latifolia* at six heights at Saturday Creek, British Columbia, in 1995 and 1996.

Capture date	*Dpon*	*Ipin*	*Pkne*	*Hpor*	*Tlin*
		1995			
145	0.00*d*	1.00*d*	1.68*b*	3.84*a*	6.16*a*
163	0.00*d*	0.84*d*	0.68*b*	2.52*ab*	1.84*b*
177	0.00*d*	1.52*d*	0.52*b*	1.32*bc*	2.52*b*
192	1.00*d*	5.68*d*	4.84*b*	0.52*c*	1.00*b*
211	14.52*c*	16.00*c*	48.16*a*	0.68*c*	1.00*b*
226	43.64*a*	3.44*a*	6.08*b*	0.16*c*	0.16*b*
241	25.00*b*	0.84*b*	2.84*b*	0.00*c*	0.00*b*
255	1.00*d*	1.32*d*	1.68*b*	0.00*c*	1.00*b*
		1996			
150	0.00*b*	21.84*b*	19.68*b*	8.00*a*	6.00*a*
163	0.16*b*	30.44*b*	42.60*b*	5.72*a*	0.68*b*
179	0.16*b*	9.76*b*	12.16*bc*	0.88*b*	0.68*b*
190	1.00*b*	15.52*b*	18.84*b*	1.80*b*	0.32*b*
202	3.44*b*	6.48*b*	10.84*bc*	0.00*b*	0.00*b*
221	20.44*a*	11.36*a*	13.68*bc*	2.00*b*	0.00*b*
233	33.20*a*	20.52*a*	7.32*bc*	0.20*b*	0.00*b*
248	1.48*b*	33.68*b*	0.44*c*	0.00*b*	0.20*b*
263	3.44*b*	7.44*b*	1.16*bc*	0.00*b*	0.00*b*
282	0.00*b*	5.00*b*	0.00*c*	0.00*b*	1.00*b*

NOTE: Means are based on combined data from the two bait treatments and two trees per treatment. For each year, means within a column followed by the same letter are not significantly different (Newman–Keuls test, $P > 0.05$). Capture dates are given as julian dates. Species abbreviations as in Table 3.

thinner bark in the upper boles of trees and bark areas lower on the bole not utilized by mountain pine beetle. Resource partitioning is regulated by semiochemical signals. Ipsdienol (a pheromone component common to both secondary species) is repellent to mountain pine beetle (Hunt and Borden 1988), and ipsenol (a component of *P. knechteli* pheromone) is repellent to *I. pini* (Savoie 1996). Of the other commonly captured scolytids, *H. porosus* normally breeds in windfall and in the roots and root collar region of dead or severely weakened trees (Safranyik *et al.* 1999). The ambrosia beetle, *T. lineatum*, normally breeds in the sapwood of windfall and trees that have been dead for at least 3 months (Shore and McLean 1995).

All of the traps in 1995 and two sets of traps in 1996 were hung from trees that had been killed by mountain pine beetle in the previous year and currently contained bark beetle broods (brood trees). The question arises whether the trap catches reflected the relative abundance of beetles emerging from, or attacking, these trees, or the relative abundance of dispersing beetles in the area, or a combination of these populations. This study was not designed to provide clear answers to this question.

The following results suggest that the vertical distribution of captures of the five abundant species reflects the vertical distribution of the respective dispersing populations. There was no interaction between treatment and capture height, hence the relative density of beetles captured at the different trap heights was not affected by the bait treatments. Except for the mountain pine beetle and *I. pini* in 1996, treatments did not

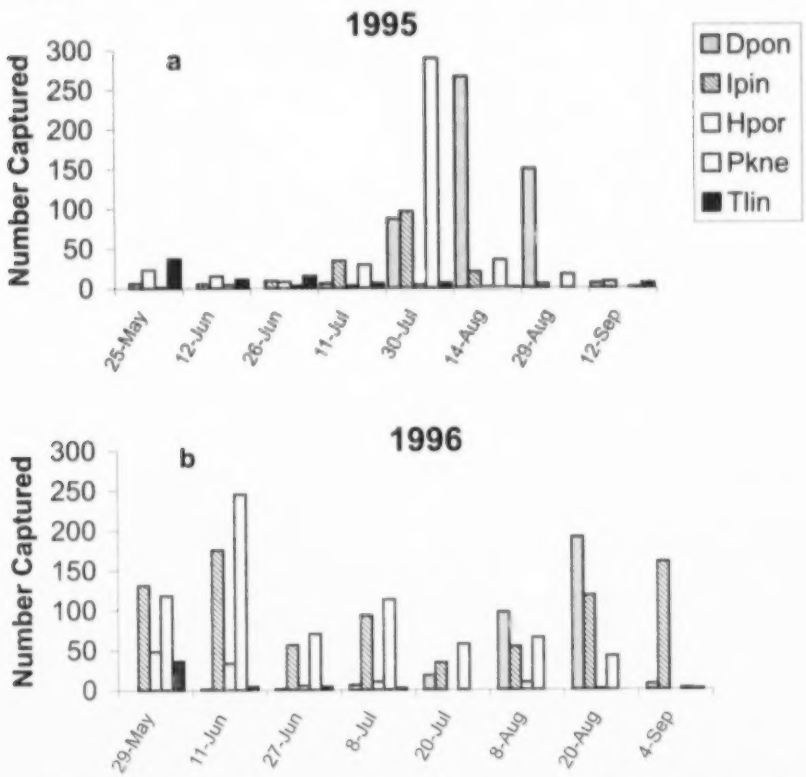

FIGURE 1. Numbers of the five most abundant scolytid species captured in flight-barrier traps in 1995 (*a*) and 1996 (*b*). Bars represent total catches in columns of six traps suspended from four *Pinus contorta* var. *latifolia* (see Table 4 for trap heights). *Dpon*, *Dendroctonus ponderosae*; *Hpor*, *Hylurgops porosus*; *Ipin*, *Ips pini*; *Pkne*, *Pityogenes knechteli*; *Tlin*, *Trypodendron lineatum*.

affect the mean numbers of bark beetles trapped. The significant interaction of treatment with trapping date indicated that more mountain pine beetles and *I. pini* were captured earlier in traps attached to mountain pine beetle brood trees than those attached to nonbrood trees. This implies that traps attached to brood trees intercepted significant numbers of mountain pine beetles and *I. pini* as they dispersed from those trees.

Although the columns of traps were hung close to tree boles, the vertical distribution of captured scolytids may not correspond closely to the vertical distribution of emerging or attacking beetles. Beetles disturbed (by predators, moving shadows, *etc.*) while on the bark may fall to the ground and fly off, land again on a tree, or walk to the base of a tree and climb various distances before initiating attacks. Most scolytids require bark scales, crevices, or furrows in which to start galleries; thus, bark roughness and thickness are major factors in determining the distribution of attacks. Due to these behavioural traits, the peak mountain pine beetle attack density is normally found at a lower height than the peak density of beetles captured in traps (Avis 1971; Safranyik 1971).

There was much overlap in the vertical distribution of the three species, although the mean heights of capture for *I. pini* and *P. knechteli* were significantly higher than those for the mountain pine beetle in both years. *Ips pini* and *P. knechteli* infest islands

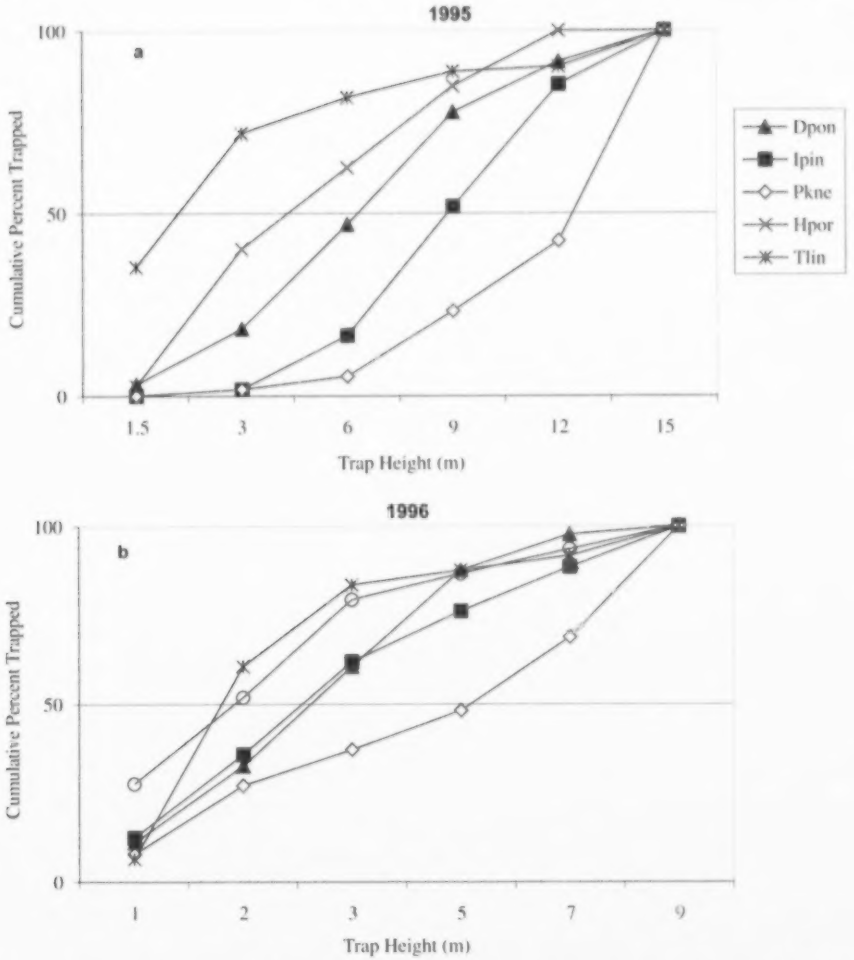

FIGURE 2. Cumulative captures of the five most abundant scolytid species in 1995 (*a*) and 1996 (*b*). Bars represent total catches in columns of six traps suspended from four *Pinus contorta* var. *latifolia* (see Table 4 for trap heights). Species abbreviations as in Fig. 1.

of unoccupied phloem on the lower bole of trees attacked by mountain pine beetle and the upper bole and larger branches. Being the more aggressive species, *I. pini* infests bole areas among those colonized by mountain pine beetle soon after the tree has been killed and attacks the upper bole early in the following year (Safranyik *et al.* 1999). *Pityogenes knechteli* mainly infests thinner bark in the upper bole and branches. The vertical distributions of *I. pini*, *P. knechteli*, *H. porosus*, and *T. lineatum* thus reflect their respective niche preferences. The optimum capture height for *T. lineatum* on baited sticky traps (1–2.5 m) reported in Shore and McLean (1984) is in good agreement with our results (Table 4).

The average emergence date for mountain pine beetle was the latest among the five abundant species in both years and was not different between years (Table 1). Emergence and flight are temperature dependent (Safranyik 1978; Safranyik and Linton

1993). A main factor of the asynchrony of mean dates of capture of mountain pine beetle and the other species was difference among species in emergence and flight in relation to temperature. Safranyik and Linton (1993) found that daily captures of mountain pine beetles, *I. pini*, and *P. knechteli* rose with average temperatures, and the greatest catches of all three species occurred when the average daily temperature was higher than 20°C for at least three consecutive days. Catches of the two secondary species peaked a day later than that of the mountain pine beetle. Catches of *I. pini* and *P. knechteli* were correlated, but there was no correlation between catches of mountain pine beetle and *P. knechteli*, and the correlation between *I. pini* and mountain pine beetle was weakly significant (Safranyik and Linton 1993).

The other main factor that affected the mean dates of capture is the difference in life histories. In the experimental area, mountain pine beetle has a 1-year cycle, with the main flight occurring in midsummer. Greater catches of mountain pine beetle have been reported at mid-bole than in the upper and lower regions of the bole (Schmitz *et al.* 1980) and were attributed to less interference from shrubs at lower levels and from tree branches higher up. *Ips pini* made two dispersal flights per year, the first by overwintered adults emerging from duff during May and June. The second flight was made during July and August by reemerging parents and brood adults from the May–June flight. Because *P. knechteli* overwinters both as larvae and as adults (Reid 1955), this species also had a spring and a summer flight. The second flights of both species occurred during the flight period of the mountain pine beetle (Fig. 2). *Trypodendron lineatum* adults overwinter in duff on the forest floor and emerge in the spring to search for host material. The mean and peak dates of flight occur in the spring. Because *H. porosus* overwinter in both the larval and adult stages, they fly throughout the spring and summer. The peak and mean dates of capture in both years occurred in the spring (Fig. 2) and indicate that this species developed in mixed 1- and 2-year cycles and overwintered mainly in the adult stage.

Our results indicate that the large number of scolytid species associated with the mountain pine beetle may be divided into two groups based on their host requirements. Those for which lodgepole pine is not a host or is just an occasional host form one group, and were captured in low numbers. The second group consists of those species for which lodgepole pine is a main host. Of this latter group, the species preferring freshly killed trees have flight periods and attack distributions which overlap those of the mountain pine beetle and may significantly affect the survival of the mountain pine beetle.

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